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Cover. *Crotaphytys antiquus* sp. nov. Ad. ***C,*** UTEP 15900 (holotype).

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Two New *Crotaphytus* from Southern Coahuila and the Adjacent States of East-Central Mexico

Ralph W. Axtell and Robert G. Webb

INTRODUCTION

During the summer of 1977 Eric C. Axtell and the authors first visited a small, rugged, isolated limestone mountain range a few kilometers northeast of Torreón, Mexico. The first vertebrate observed (on rock outcrops) was a bright green lizard with a dark collar. We realized immediately that this was an unknown *Sceloporus* that would eventually need description (now in preparation). Later that same day Webb took a juvenile female *Crotaphytus* that was also recognized as being very different. We had no further encounters with this *Crotaphytus* in 1977, but in 1978, we returned to the same area, where E. Axtell collected the first adult male on June 20. On this, and three subsequent visits (1979 1980, and 1982), the three of us obtained 20 additional specimens from this and two other small ranges nearby.

This remarkable new lizard displayed characteristics much like C. *reticulatus,* found approximately 300 kilometers to the east northeast, but it also shared features with populations of *Crotaphytus* that occur over 800 kilometers away in Sonora, Mexico! In order to accumulate an adequate sample, and not adversely affect the populations, we collected small numbers each year until we could no longer afford to obtain permits. Because these lizards are restricted to such a small geographic area, and because they occur so close to a major population center, R. Axtell decided, with the reluctant concurrence of Webb, against formal description for conservation reasons. We decided that formal descriptions would be postponed until circumstances warranted. In 1994, we learned that other herpetologists had visited the ranges involved, so we suspected that our earlier discovery was no longer confidential. Because we can no longer consider conservation by silence a viable option, we take this opportunity to describe this new collared lizard as:

Crotaphytus antiquus **sp. nov.**
Venerable Collared Lizard

Holotype. The University of Texas at El Paso (UTEP) 15900, an adult male obtained at 2.1 km N-1.7 km E Vizcaya (25° 46' 04" N-103° 11' 48" W, el 1100 ± m) in the Sierra Texas, Coahuila, Mexico, on 22 June 1978, by E.and R. Axtell; originally RWA 6537.

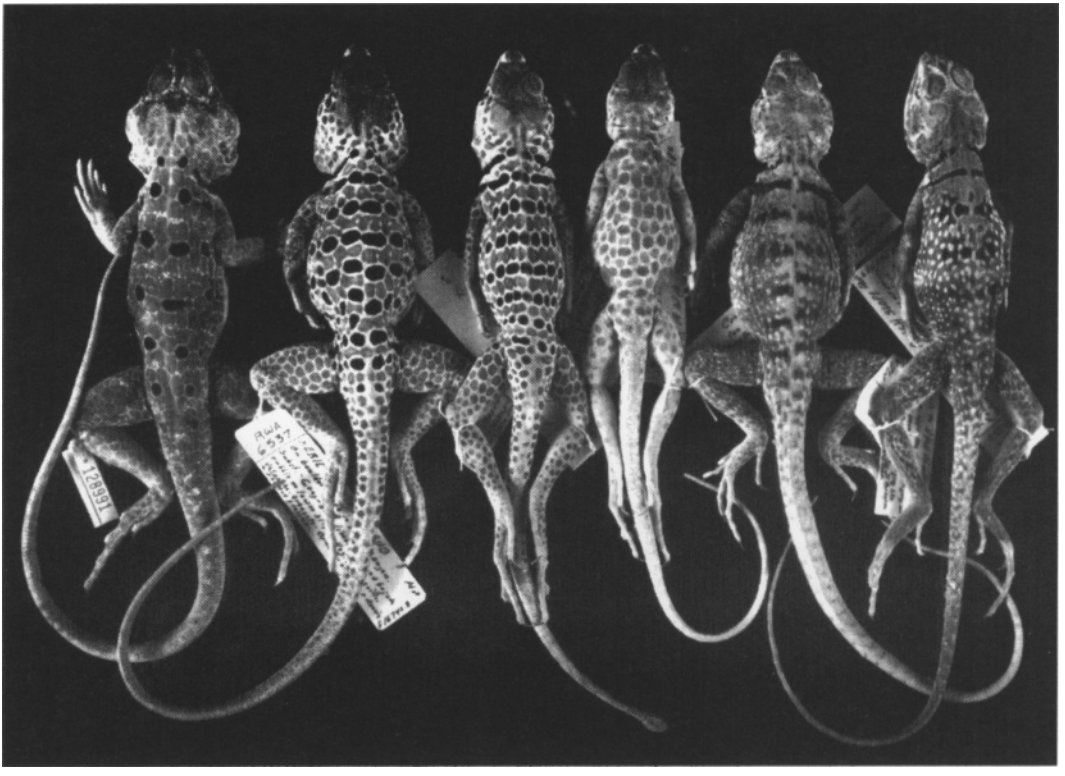

Figure 1. Dorsel view. From left to right: *Crotaphytus reticulatus,* Ad *d,* KU 128991; C. *antiquus* Ad *d',* UTEP 15900 (holotype; large spotted form); C. *antiquus* Ad *d,* RWA 6369 (small spotted form); C. *antiquus;* Ad 9 , RWA 6320; C. *c. melanomaculatus,* Ad 9 RWA 6542; C. *c. melanomaculatus,* Ad *d,* UTEP 15915 (holotype).

Paratypes. 21 (12 *d',* 9 9), as follows: RWA 5677-79, 5687-88, 5698, 5707, 5947, 6122, 6317-19, 6369-73, 6538-39, and RGW 6695.

Diagnosis. A taxon of the genus *Crotaphytus* characterized by (both sexes included unless otherwise indicated): a third scale row between the supraorbital semicircles; no melanic pigmentation on the oral-pharyngeal floor and fauces; no dark pigmentation pattern on crown or adjacent temporal region of either sex; sides of head and lateral temples patterned with dark spots; no conspicuous yellow lipophore or green or blue iridophore pigmentation; a cross-banded dorsal pattern of seven or eight rows (collars included) of bold, black, light-margined spots or short, rounded dashes in adult males, and a similar pattern, but largely lacking the black, in adult females and young; rounded to angular tan markings between the black-spotted crossbands in mature males (a similar pattern, but less distinctive in females and young); a complete or nearly complete melanic gular collar

in adult males; bluish-gray coloration of central gular region usually invaded posteriorly by a dark, forward-pointing melanic wedge in adult males; no pale speckling on dorsal trunk, limbs, or tail in either sex; deep postfemoral dermal pockets present; jet black femoral pore plugs in mature males (not as dark in females and young); conspicuous melanic patches on proximal anteroventral surfaces of femora in mature males; no melanic suffusion across anterior and lateral chest region; tail in adult males laterally compressed for entire length; and a series of paired, dark pigmented, keeled scales on ventral caudal extremity.

Description of Holotype. (all measurements in mm). Dorsal crown scales highly elevated, convex, and often with angular edges (rugose); rostral small (1.62 high by 3.8 wide); four postrostrals; six anterior, six median and six posterior internasals, with slight enlargement of left median series; greatly enlarged median scales posterior to central postrostral and central internasals; six frontonasals (in transverse row between posteriormost canthals); 10-10 circumnasals; 10 scales between rostral and anterior convergence of enlarged supraocular semicircles; 17 median scales between rostral and interparietal (this count uninterrupted by semicircle convergence); interparietal small (2.18 long by 1.47 wide) with parietal lens slightly posterior to center; posterior edge of parietal shelf six scales posterior to interparietal; lateral parietals larger than most other anterior semicircle scales, but same size as or slightly smaller than lateralmost frontonasals (anterior part of semicircles), median parietals much smaller (ca. 5% to 8% of interparietal size); transverse parietals between postocular tubercles, 11; supraoculars granular (ca. same size as or slightly smaller than dorsal trunk scales), and slightly enlarged in median ocular area, but more enlarged anteriorly and laterally (transverse count across widest part of orbital region, 10 lt-9 rt); superciliaries 9-9 (short, but overlapping); 4-4 canthals, the posteriormost largest; entire protuberant infraocular series with eight scales on both sides (3-3 anteriorly, 1-1 elongate suboculars, and 4-4 posteriorly); lorilabials from posterior canthal to supralabials directly below, 8-7; fewest scale rows between nasal and supralabials, 2-2; fewest scale rows between subocular and supralabials, 3-3; scales between postocular tubercles (at posterolateral edge supraocular semicircles) and upper jaw margin, 14-14; supralabials (to opposite last enlarged infralabial below), 11-14. Dorsal temporal scales slightly larger than surrounding head scales and strongly conate; median scales over parietal shelf less than half size of laterals; lateral temporals become smaller and more convex ventrally; anterior auriculars about twice size of posterior auriculars; auricular opening somewhat constricted by nuchal skin folds (opening 5.4 high by 1.0 wide).

Mental pentagonal (widest part opposite anteriormost labiomental) and somewhat wider (3.64) than deep (2.59); postmentals slightly less than half size of mental and in medial contact; both postmentals separated from anterior infralabials by lateral labiomental; anterior chinshields separated medially by two enlarged anterior gulars; two rows of chinshields anteriorly, rapidly decreasing in size and merging with gulars posteriorly; infralabials 14-12 (scar between second and fourth infralabial makes count inaccurate); gulars unkeeled, strongly conate posteriorly, becoming weakly imbricate only in area near gular fold; symphysial depression vestigial; most of gular area showing lesion from fungal infection suffered before preservation.

Dorsal scales of trunk rounded, smooth, convex, and nonimbricate, with minute intervening tubercles; median dorsals of midback slightly larger (1.5-2X) than nuchals and laterals; dorsals from interparietal to opposite anterior junction of hindlimb with trunk, 142; two tranverse folds extending across gular region, a partial anterior fold (flattened posteriorly due to preservation) with no difference in scale size, and a complete posterior fold, with larger granules anteriorly changing to smaller posteriorly (this fold extends dorsally over the foreleg to form a deep suprabrachial pocket that terminates to rear of limb).

Ventrals smooth, flat, and slightly imbricate, largest on belly (3X to 4X size of adjacent laterals), becoming smaller in sternal and sacral regions and smallest around posterior limb junctions; a weakly defined lateral fold, with no change in scale size, extends from behind axilla to in front of groin; 95 median ventrals from posterior edge gular fold to edge cloacal lip.

Dorsal and lateral caudals subequal in size and slightly smaller than ventral caudals; transition from dorsal trunk scales to caudals begins immediately posterior to sacrum; proximal dorsal caudals remain smooth but become slightly imbricate, more quadrangular in shape, and larger (ca. 2X size) than dorsal sacral scales; dorsal keeling begins weakly on distal two-thirds of tail but becomes more prominant on distal third (small terminal mucrones appear on distal 2 cm of tail); postanals slightly enlarged (8 scales) and in single transverse row; a deep postfemoral dermal pocket on posterodorsal junction of hindlimb and trunk.

Scales on lateral surface of forelimbs weakly imbricate with slight keeling above wrist; medial scales become nonimbricate and more granular; largest scales of forelimbs on distal dorsal surfaces of digits and on anteromedial distal half antebrachium above first and second fingers; scales on upper surface of manus smooth to slightly concave and weakly imbricate; scales on palmar surface of manus more strongly imbricate and angular, with multiple keels (1-3) and stubby terminal mucrones; subdigital scales weakly imbricate with three to five low keels armed with short terminal mucrones.

Scales on anterior surface of thigh, over knee, and on anteroventral shank largest scales of hindlimb (all weakly convex, smooth and slightly imbricate); anterior thigh scales (up to 4X dorsal thigh scales) grade into granules on top and rear of thigh, and to smaller imbricate scales anterior to enlarged pore series, then rapidly decrease in size posterior to pore series; 19-19 dark pigmented femoral pores; scales on anteroventral shank largest (2X to 6X size dorsal femorals), smooth and moderately imbricate; dorsal scales of pes slightly imbricate, smooth to slightly concave with few apical organs mostly on distal metatarsal region; largest scales on anteroventral face of ankle region and on anterior and dorsal faces of digits (dorsal terminal and penultimate scales of digits also considerably enlarged, their terminal scales elongate and clawlike); scales on plantar surface of pes strongly imbricate, angular, with one to three low, rounded keels terminated with stubby mucrones; subdigital lamellae slightly to moderately imbricate with three to five rounded keels (many terminated with dark conate mucrones); lamellar count for left foot (to most distal junction point with adjacent digit; hallux first): 12, 17, 24, 35, 18.

Measurements (in mm). Snout to vent, 102; snout to posterior edge interparietal, 22.26; interparietal length, 2.33; mid-snout to bony contact anterior edge orbit, 11.13; snout to ventral margin auricular depression in bony quadrate, 31.2; transverse distance between outer edges nasals, 7.41; transverse distance between outer edges posterior canthals, 11.41; transverse distance between lateral edges postocular tubercles, 16.14; widest distance across head, 25.35; highest point on top head to ventral edge mandible with mouth closed, 17.24; tip snout to anterior base bony coronoid with mouth closed, 17.55; forelimb from posterior axilla to digit tip, exclusive of claw, 42.7; posterior junction hindlimb to tip fourth digit, exclusive of claw, ca. 87.8; fourth toe length from junction angle with third toe, exclusive of claw, 20.5; cloacal lip to tail tip, 231; tail width one foreleg length posterior to cloacal lip, 7.28; tail height one foreleg length posterior to cloacal lip, 8.78; tail width into height, 1.21.

Coloration (in alcohol and in life; mainly colors described below, see figures for pattern). Crown and upper temporal region uniform dusky brown; spots on sides and rear of head tannish-gray, to brown to almost black on a pale creamish ground; (posterolateral temporal region, sides of neck and anterior trunk pale peach in life); transverse rows of spots black dorsally, becoming brownish to pale tan or gray laterally (each dark mark surrounded by white margin); areas on trunk between dark spots (with their pale borders) filled with grayish-tan markings of varying shapes (these interstitial markings continue onto tail, where they become darker caudal spots on a creamish-tan ground); dorsal fore and hindlimbs with pale grayish-tan spots (decreasing in size distally) on a paler dirty cream ground (a few brownish-black spots occur on the proximal sections of both limbs); chin and jaw regions with gray to brownish-gray markings anteriorly and laterally changing to grayish-blue centrally; melanin pigment of gular collar extends anteriorly as dark wedge; chest, belly, interfemoral area, and much of ventral surfaces of limbs, plus all of tail, opaque white (except for scar tissue discolored from fungal infection while in captivity); anteroventral surfaces of each thigh marked by bold, black blotches that have thin connections with dark transverse trunk spots in groin region.

Variation Few of the diagnostic characters vary, as most are either present or absent in *C. antiquus*. The third row of interorbitals is complete in seven males and seven females, incomplete in four males and two females, and indeterminate in one injured individual. Only one scale is missing in all specimens having incomplete rows. Several specimens have what appears to be an asymmetric fourth row posteriorly. The summed femoral pores vary from 33-40 ($306.50 \pm$ SE 0.387, N = 22). Two pattern morphs are represented in adult males; one morph has slightly larger and fewer black spots than the other (see Figure 1). Three males of the 12 display the larger spot feature; one is the holotype.

Mature females and juveniles are dimorphic in morphology and in color pattern. The head is narrower and the tail is less compressed in both. Females and young do not display the distinctive black spotting of adult males (spots are pale to medium tan), and they lack the elaborate interspot pattern of the males. The gray-blue gular patch, the black gular collar, and the dark subfemoral blotches are all absent in females and young. One distinctive feature shared with males is the black femoral pores (although the pigmentation is not as intense).

Distribution. As far as we can determine, this species is restricted to three small ranges (Sierra Texas, Sierra Solis, and Sierra San Lorenzo) in the Mayrán or Parras Basin of southwestern Coahuila, Mexico. This apparent isolation has an explanation that may not be obvious to the casual observer, because humans have extensively altered the area by agricultural activities, and because the climate has probably become more xeric in the recent past. Looking at the map (Figure 4) it appears that two major rivers, the Rio Aguanaval from the south, and the Rio Nazas from the southwest, flow northward into the Mayrán Basin. Flow from the Aguanaval now terminates in irrigation canals south of the ranges where C. *antiquus* occurs, and flow from the Nazas now ends in a dry playa area (and in irrigation canals) north of these ranges. Before humans altered the area, both rivers flowed into a large lake called the Laguna de Mayrán (shown on many older maps; also, see Montanucci 1974) that probably expanded and contracted as the climate changed. Had it not been for the isolating capacity of water and the fortunate circumstance of initial occupation by this lizard, we would not have had this fortunate window to the past. Instead, we would have had to contend with the perplexing problem that faced Montanucci (1974 and see below), that is, how to make sense of such a peculiar distributional situation. See Axtell (1977) for other examples of isolation by water in the southwest.

Etymology. *Antiquus* is a Latin word for old; this choice incorporates our interpretation regarding the probable ancientness of this lizard. The meaning is reflected in both the scientific and vernacular names chosen.

Populations of C. *collaris* completely surround the island-like ranges occupied by C. *antiquus*. Montanucci (1974) characterized and discussed the relationships of these Coahuilan populations without giving them a formal name. Because his use of the common name—black-spotted collared lizard—probably involved several different diagnosable entities, we formally name the black-spotted form so that reference to it in subsequent text, and in our combined comparisons and relationships sections will be unambiguous.

Crotaphytus collaris melanomaculatus **ssp. nov.**
Black-spotted Collared Lizard

Holotype. The University of Texas at El Paso (UTEP) 15915, an adult male obtained at 25° 14' 10" N-103° 47' W or 3.8 km S-1.7 km E Graseros on the highway to Presa Francisco Zarca, el 1250 ± m, Durango, Mexico, on 6 July 1982, by E. C. Axtell; originally RWA 6541.

Paratypes. 33 (15 **c[r],** 18 **9),** as follows: RWA 1794, 3877, 4119, 5043, 5123-27, 5258, 5686, 5693, 5706, 5723, 5759, 5801, 5850-51, 5943, 5955, 6286, 6293, 6389, 6540, 6542, UTEP 4556-60, 6849, 8708, 9416 (numbers in series do not imply same collection sites).

Diagnosis. A subspecific taxon of the genus *Crotaphytus* characterized by (both sexes included unless otherwise indicated): two rows of enlarged supraorbital semicircles contacting between

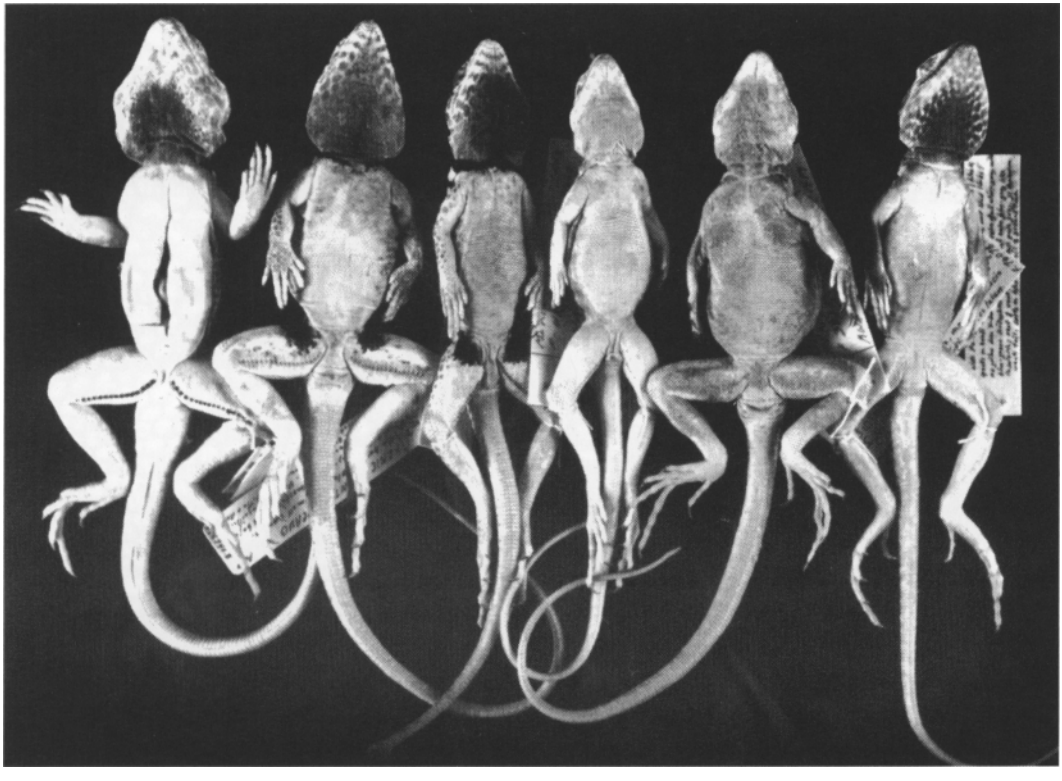

Figure 2. Ventral view. Arrangement same as in Figure 1.

orbits; melanic pigmentation on the oral-pharyngeal floor and fauces; melanic specks, spots, or lines on crown, temporal region, and sides of head; no complete melanic gular collar or black gular salient directed anteriorly; yellow lipophore pigments and/or green iridophore pigments present on trunk or limbs; a dorsal trunk pattern (including collars) of five to seven black irregular crossbands, or crossbands consisting of several squarish or rounded black spots variously margined with pale broken dashes or small spots; no background of discrete rounded or angular pale tan or gray markings between dark crossbands; dorsal fore and hindlimbs variously patterned, but never with discrete darker spots on a uniform paler tan ground; femoral pore plugs in mature males not pigmented, or, if pigmented, only slightly so (never jet black); no conspicuous black patches on proximal, anteroventral surfaces of femora in mature males; and summed femoral pores 34-46 ($^{g}41.39 \pm$ SE 0.47, N = 33); no, or very few, paired, dark pigmented keeled scales on ventral caudal extremity.

Abbreviated Holotype Description (all measurements in mm; only features generally unlike those found in C. *antiquus* are included here). Dorsal crown scales moderately elevated, convex, with slightly angular edges (moderately rugose); rostral small (2.63 wide by 1.27 high); eight fron-

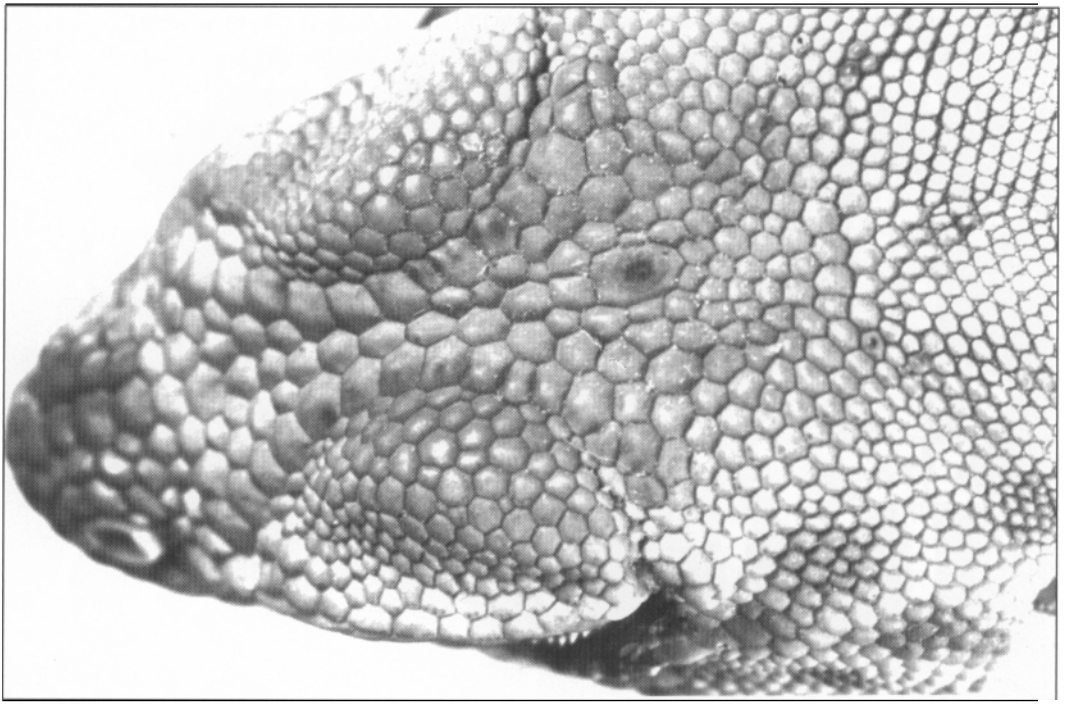

Figure 3. Dorsal head of Ad Q *C. antiquus* (RWA 5679) showing third row interocular scales.

tonasals between posteriormost canthals; 11-11 circumnasals; 10 scales between rostral and anterior confluence of supraocular semicircles (three pairs of supraoculars in medial contact, with azygous scale interposed between first and second pair); interparietal 1.71 long by 1.32 wide, with parietal lens in center of long axis; transverse parietal count (between postocular tubercles), 16; 9-10 superciliaries, with medial superciliary very elongate; scale rows above superciliary rows superciliary-like and also with a very elongate scale; protuberant infraocular series extended, with 10-11 enlarged scales (3-3 anteriorly, 1-1 central, and 6-7 posteriorly); scales between postocular tubercle and upper jaw margin, 17-17; dorsal temporal scales same size as, or slightly smaller than, surrounding head scales and moderately to weakly conate; lateral temporals about same size as dorsal temporals and of same convexity; anterior auriculars ca. 3X to 4X size of posterior auriculars; auricular opening moderate in size (1.61 wide by 5.15 high) and not obscured by skin folds.

Mental pentagonal and slightly wider (2.48) then deep (2.18); postmentals about 60% to 65% size of mental, and contacting anterior infralabials; infralabials 13-12; symphyseal depression weakly developed, but not vestigial.

Dorsals from interparietal to opposite anterior junction hindlimb with trunk, 136. Ventrals slightly imbricate and smooth, with hint of keeling; ventral scales smaller on sternal and anterior sacral regions, but slightly larger in precloacal region; midbelly scales 3X to 5X size of adjacent granular laterals; 113 median ventrals from opposite posterior edge gular fold to edge cloacal lip.

In contrast to trunk scales on dorsal sacral region, proximal caudals more quadrangular and weakly imbricate; weak dorsal keeling begins about 3 cm (laterally and ventrally ca. 12 mm) posterior to hindlimb junction and becomes increasingly acute distally; small terminal mucrones appear on proximal half of lateral and ventral tail and become increasingly spinose distally; six pairs of keeled scales on tail tip slightly tinted with tan pigment; postanal scales moderately enlarged and in double transverse rows of 11-10 scales.

Enlarged scales of thigh and shank smooth, but with traces of median curvature that resemble incipient keels; femoral pores, 20-21, with no trace of dark pigmentation; scales on dorsal surface of pes slightly imbricate and weakly but clearly keeled (with few apical organs, mostly in mid-metatarsal region); scales on plantar surface of pes moderately imbricate, angular, and with three to six obtuse keels (terminated without or with very weakly pigmented conate mucrones); lamellar count for left foot (to most distal junction with adjacent digit; hallux first): 10, 15, 23, 35, 15.

Measurements (in mm). Snout to vent, 99.9; snout to posterior edge interparietal 19.95; interparietal length, 1.74; midsnout to bony contact at anterior edge orbit, 10.07; snout to ventral margin auricular depression in bony quadrate, 28.84; transverse distance between outer edges of nasals, 6.77, between outer edges posterior canthals, 10. 54, and between lateral edges postocular tubercles, 15.18; maximal head width, 24.28; greatest distance between top head and ventral mandible with mouth closed, 14.66; length foreleg from posterior axilla to digit tip (exclusive of claw), 42.87; posterior junction hindleg to tip fourth digit, 87.70; length fourth toe from junction with third toe, 20.55; cloacal lip to tail tip, 213; tail width one foreleg length posterior to cloacal lip, 5.58; tail height one foreleg length posterior to cloacal lip, 6.47; tail width into tail height, 1.16.

Coloration (in alcohol and in life). Entire cranium pale gray to tannish-gray, with small, unconnected melanic specks forming indistinct radiations below eyes, postocular stripes and other ill-defined marks; sides of mandibles with posteromedially converging chevrons formed from gray spots (becoming darker medially until they merge with blue-gray of central gular area); dark gular color stops several scales anterior to posterior gular fold; nuchal region between black collars and V-shaped area on anterior dorsal trunk dusky gray with few other marks; two black collars plus four transverse crossbands of black squarish to rounded spots on trunk, with one additional pair of spots over sacrum; circular to slightly elongate white spots (1-3 mm across) commence posterior to V-shaped gray area on anterior trunk (these encircle dark marks and punctuate darker olive-gray on posterior back and flanks); lower flanks and edges of belly weakly tinted with bluish-green in life; pale spotting continues over pelvis and onto base of tail where it abruptly changes to irregular dark marks on a paler gray-tan ground; forelimbs marked with obscure, small, dusky spots on a gray ground; hindlimbs speckled with white marks proximally, but changing distally to dark spots

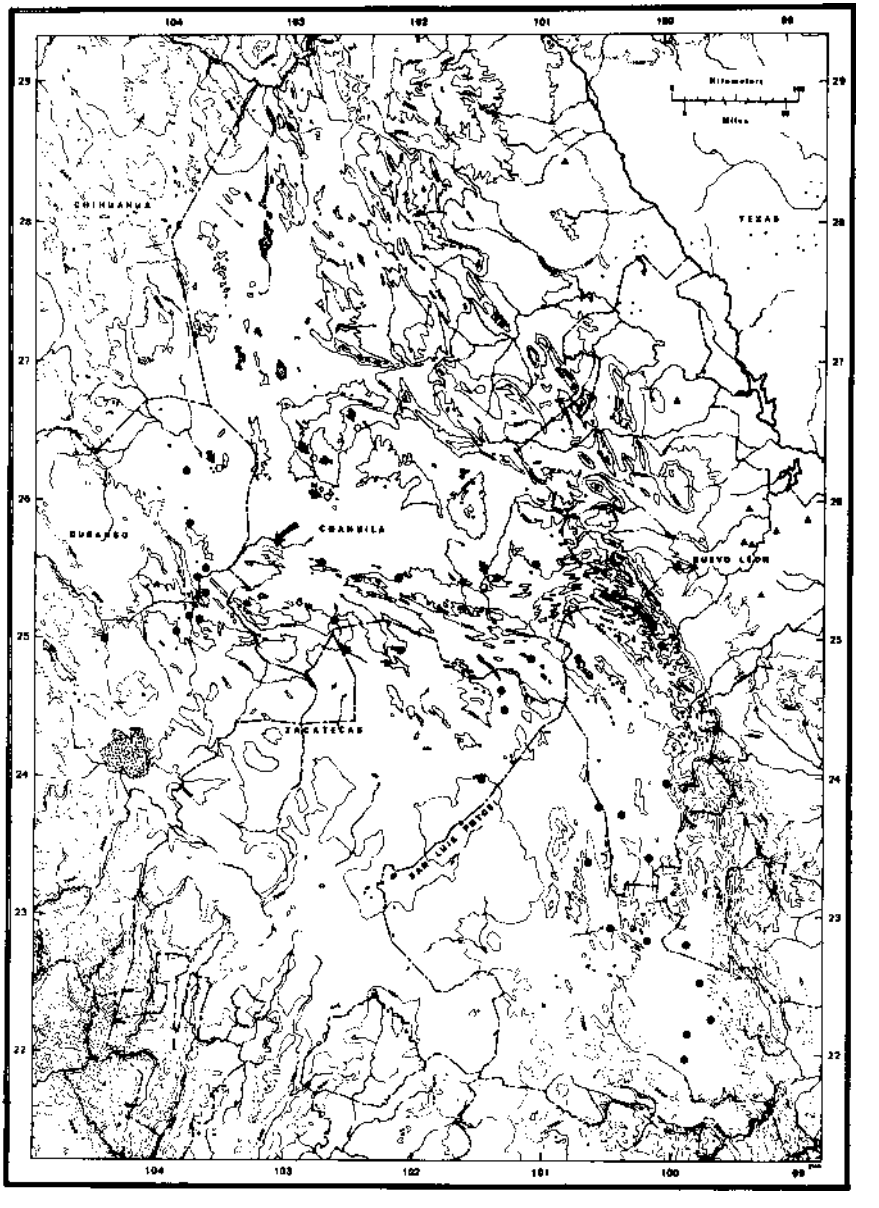

Figure 4. Map of northeastern Mexico showing ranges inhabited by C. *antiquus* (large, curved arrow), type locality for C. *c. melanomaculatus* (large, straight arrow and black star), plus several other localities for this taxon (black dots). Certain adjacent localities for unspotted *C. collaris* (open circles with short black arrows), and for C. *reticulatus* (black triangles) added to show spacial relationships. Map adapted from Jet Navigation Chart (JNC 46), scale 1:2,000,000. Dotted contour lines at 1,000, 3,000, 5,000, and 7,000 feet.

on olive-gray ground (in life, both fore and hindlimbs tinted with yellow); entire ventral surface dull grayish-white (tail sligthly darker) with no dark femoral pores or groin markings.

Variation. The interorbital scales of C. *c. melanomaculatus* indicate how earlier hybridization with *C. antiquus* may have affected this lizard. The scales are variable in form and number (no general pattern), have fairly frequent interstitial or azygous scales (5 of 15 males, 4 of 17 females) between the interorbitals (of rare occurrence in other *Crotaphytus),* and many (7 of 15 males and 8 of 17 females) have more than three frontoparietals (from contacting semicircle rows to interparietal), whereas one or two frontoparietals is the usual count in most C. *collaris* populations.

The morphology of the transverse black markings is highly variable, from irregular crossbars, to squarish spots (most frequent) to rounded spots similar to those in C. *antiquus.* Montanucci (1974) reported unspotted specimens within the region where this lizard occurs, but we have none of these in our sample (almost all personally collected). The general body coloration in this lizard resembles that seen in adjacent (to the north, east and west) populations of C. *collaris* more than that in *C. antiquus.*

Both limbs and body frequently show yellow lipophore pigmentation, although green and blue iridophores appear rarely. All samples thus far examined exhibit the pale (white or yellow) dorsal speckling characteristic of C. *collaris,* but there is considerable variation in the size and distribution of these marks on the trunk. One large male from near Ahuichila, Coahuila (RWA 5693) has black femoral speckling in the same position as the vivid black subfemoral patches in male C. *antiquus.*

The femoral pores are variable in the amount of melanin in the pore exudate. In most individuals no pigment is visible; in others (only males), a few specks of pigment are visible, but in one male (RWA 5686) from Zacatecas, the margins of the pore exudate are heavily pigmented. In no specimens, however, are the pores totally black as they are in C. *antiquus.* The summed femoral pore counts vary from 34 to 46 (R41.39 ± SE 0.47, N = 33), considerably higher than in either C *antiquus* (see above) or in C. *reticulatus* (see Montanucci 1974).

Distribution. *C. c. melanomaculatus* occupies many of the ranges to the southwest, south and southeast of the small group of ranges occupied by C. *antiquus* (see Figure 4). Occurrence to the southwest includes the Rio Nazas and some of its tributaries. To the south, populations are known from the Pedriceña region, and to the east populations occur, perhaps discontinuously, along the northern front of the Sierra de Parras and other smaller ranges, to the vicinity of General Cepeda where they may contact other populations of C. *collaris* that are not black-spotted (see Figure 4). Most of the range, however, coincides with a series of elongate basins, with bordering ranges, that extend from southwestern Coahuila southeastward through the states of Zacatecas, Nuevo Leon, and San Luis Potosi, to the southwestern edge of Tamaulipas (see Figure 4).

Etymology. *Melanomaculatus* comes from the Greek *melaina* meaning black, and the Latin *macula* meaning spotted.

COMPARISONS BETWEEN THE SEVERAL TAXA

C. antiquus has the following characters that are found in neither C. *collaris melanomaculatus* nor in C. *reticulatus,* but are of variable occurrence in certain western *Crotaphytus* taxa: three complete or almost complete rows of interorbitals (shared with some C. *dickersonae);* no oral melanin (shared with three C. *insularis* ssp. and with C. *dickersonae);* no green or blue iridophores in either sex (also none in three C. *insularis* ssp.); a complete or nearly complete melanic gular collar in adult males (shared with three C. *insularis* ssp., C. *dickersonae* and C. *collaris nebrius;* melanic patches on anteroventral proximal femur of adult males (shared with three C. *insularis* ssp., and C. *dickersonae);* and two rows of keeled, dark-tipped scales beneath distal tail (shared with three C. *insularis* ssp. and with C. *dickersonae).*

C. reticulatus has the following characters that are shared with C. *antiquus* but not with C. *collaris melanomaculatus:* zones between dark spots of adult males filled with discrete circular to angular tan (in C. *antiquus)* to darker grayish-tan (in C. *reticulatus)* markings; and black femoral pores (although some melanin speckling is present in the pore exudate of many male C. *c. melanomaculatus). C. reticulatus* differs from all other *Crotaphytus,* and from *Gambelia,* in lacking a post-femoral dermal pocket.

C. c. melanomaculatus often shares the following characters with C. *antiquus,* with the three western C. *insularis,* and with C. *reticulatus:* central gular area in adult males solid grayish-blue; darker round spots (on a paler ground) on lateral gular area and on more distal parts of limbs; and some lateral compression of tail (most other C. *collaris* ssp. have little or no tail compression). It shares the transverse rows of dark spots or crossbars on the neck, trunk, and base of tail only with C. *antiquus* and C. *reticulatus* (although this feature occurs haphazardly in other C. *collaris,* and in the young of most *Crotaphytus* species).

PROPOSED RELATIONSHIPS OF BOTH NEW TAXA

The several characteristics, enumerated above, that serve to link C. *antiquus* with the far western members of the genus *Crotaphytus* (see Montanucci et al. 1975), indicate an archaic relationship with this western lizard complex. Thus, we believe C. *antiquus* would fit, along with *Xantusia extorris* and *X. bolsonae, Uma exsul* and U. *paraphygas,* an ancient transcontinental distribution pattern that only now, with this most fortunate addition, is becoming recognizable. Perhaps now that a pattern is emerging, further examples from taxa in other groups can be identified. Because C. *antiquus* shares so many features (see above) with this western assemblage, we consider it a member, along with *C. i. insularis, C. i. vestigium, C. i. bicinctores* and C. *dickersonae,* of the *insularis* species group.

Because C. *antiquus* shares both the supernumery interocular feature (although with different sized scales) and the postfemoral dermal pocket (although more weakly developed) with both species of *Gambelia,* we consider C. *antiquus* more closely related to *Gambelia* than is C. *reticulatus,* which lacks both of these characters.

The relationship between C. *antiquus* and C. *reticulatus* is enigmatic. We consider both taxa phylogenetically and geologically old, declining, and geographically peripheral, yet both apparently are still **not genetically isolated** from other *Crotaphytus*. These two taxa have probably paralleled one another geographically for thousands or perhaps millions of years, but the barrier that has kept them separated, unless it was water (see below), is unknown. If forced to make a choice as to which is more plesiomorphic, we would choose a C. *antiquus-like* ancestor over a C. *reticulatus*-like ancestor, for we consider a C. *reticulatus-like* product derivable from C. *antiquus,* but the reverse would be difficult to imagine.

Montanucci (1974) presented both morphologic and biochemical evidence for gene flow (via hybridization) between C. *reticulatus* and adjacent populations of C. *collaris* in northeastern Coahuila, Mexico. As far as we are aware, this evidence has not been challenged or falsified. Montanucci (1974) also recognized similar hybridization evidence for the black-spotted *Crotaphytus* populations from southern Coahuila, but there was no local reservoir of the black-spotted condition there, so he hypothesized a much larger earlier range for C. *reticulatus* to explain this complication. We suggest that C. *antiquus,* instead of C. *reticulatus,* was the original local contributor of this black-spotted condition, and to numerous other intermediate conditions present in these C. *collaris* populations. All the morphological evidence we have examined supports Montanucci's (1974) hybridization hypothesis. We assume that the historic range of C. *antiquus* once must have covered considerably more area than it does today. With this in mind, we suggest the following scenario: At some time in the past, expanding populations of the widespread C. *collaris* genome entered the range of C. *antiquus* from the north (from one or more directions), and during this expansion, its populations interbred with the locals, incorporating a portion of their genes (Montanucci 1974, referred to this as introgressive hybridization, we prefer **encroachment hybridization** as a descriptor) as the invading front passed through. The moving front, now carrying a shared genetic complement (here given the name C. *c. melanomaculatus),* continued expanding beyond the original range of C. *antiquus,* into the arching ranges and basins of eastern Zacatecas, southern Nuevo Leon and central San Luis Potosi, where this lizard occurs today. If this dynamic scenario is correct, and it can be tested both morphologically and biochemically, it will seriously challenge some long-held (and more contemporary) ideas regarding differentiation in animal populations (i.e. speciation concepts).

Phylogeny. Given the information we have now, we wish to modify, for purposes of later discussion and argument, the phylogenetic tree originally proposed by Montanucci et al. (1975). We would now position C. *antiquus* as the basal member of the C. *insularis* clade, deriving this clade from a *Gambelia-like* ancestor. C. *reticulatus* would be derived from a C. *antiquus-like* ancestor, and would branch to all C. *collaris* taxa. C. *reticulatus* would also be connected by a feedback reticulation line to C. *collaris* ssp. to indicate current hybridization between these two taxa (see

Montanucci 1974). An intergroup reticulation line would connect C. *antiquus* with an unknown (see above) C. *collaris,* with which it would merge to form C. *c. melanomaculatus*. *C. dickersonae* would be moved from the C. *collaris* group to the C. *insularis* group and would be connected by a reticulation line to C. *c. nebrius,* indicating encroachment hybridization between these two forms in the past (see information in Axtell 1972, Montanucci et al. 1975, and Axtell and Montanucci 1977). C. *i. bicinctores* would be connected by an reticulation line to C. *c. baileyi,* indicating limited encroachment hybridization in the past (see Axtell 1972, and Montanucci 1983).

If the above phylogeny is near correct, it would seem that evolution in the genus *Crotaphytus* may be much more complicated than anyone has previously imagined.

SPECIMENS EXAMINED AND MAP VOUCHERS

A number of map vouchers for *C. reticulatus* and *C. collaris* have been taken from Montanucci (1974). These records are not repeated below. The **RWA** specimens are in the personal collection of the senior author; most of these will be distributed to various museums and collections emphasizing Mexican herpetology. The single **RGW** specimen will be deposited in the UTEP collection. Investigators unfamiliar with map coordinates may contact the senior author for a list of collection sites using traditional entries. Elevations (in meters), when known, follow coordinates after a comma. Seconds are deleted when the locality falls on the minute line.

Crotaphytus antiquus. **Coahuila** 25° 35' 57" N-103° 11' 57" W, 1140 (RWA 6320); 25° 36' 04" N-103° 11' 48" W, 1140 (RWA 5677-79, 5690, 6537); 25° 36' 12" N-103° 12' 03" W, 1170 (RWA 6372, 6539); 25° 36' 15" N-103° 11' 57" W, 1210 (RWA 6373); 25° 36' 16" N-103° 12' 04" W, 1220 (RWA 6318-19); 25° 36' 18" N-103° 12' 05" W, 1200 (RWA 6122, skel.); 25° 36' 20" N-103° 11' 55" W, 1250 (RGW 6695, RWA 5687-88); 25° 36' 56" N-103° 05' 57" W, 1130 (RWA 6369); 25° 37' N-103° 10' 48" W, 1130 (RWA 6371); 25° 41' 03" N-103° 14' 53" W (RWA 5707); 25° 42' 14" N-103° 07' 45" W, 1115 (RWA 5947, 6538); 25° 42' 36" N-103° 13' 35" W, 1115-25 (RWA 6317, 6370)

Crotaphytus collaris melanomaculatus: **Coahuila** 8 km NW Ahuichila (UTEP 4559); 24° 52' 20" N-101° 05' W, 1829 (RWA 4119); 25° 09' 40" N-102° 38' 55" W, 1368 (RWA 5693); 25° 11' 45" N-102° 38' 45" W, 1393 (RWA 5955); 25° 28' 30" N-101° 20' 40" W, 1372 (RWA 5258); 25° 35' N-102° 42' W, 1189 (RWA 5043); 26° 01' 45" N –102° 44' W (EAL 3178). **Durango** 4.8 km E
Mapimi (UTEP 4556); 7.2 km NE Pedriceña (UTEP 4560); 10.9 km NW Estación Chocolate (UTEP 4557); 25° 03' 30" N-104° 29' 30" 1372 (RWA 3877). **Nuevo Leon** 8.4 km by rd. S Rayones on Galeana rd. (EAL 4686); 9.5 km WNW Mier y Noriega on rd. to Dr. Arroyo (EAL 336); 23° 42' 10" N-100° 22' 10" W (EAL 4070); 23° 57' 58" N-100° 00' 45" W, 1650 (RWA 5801, 6293). **San Luis Potosi** 17.7 km SSW Ciudad del Maiz on rd to Cardenas (UTEP 6849); 14.8 km S San Francisco, S Las Tablas (UTEP 8708); 122° 10' 30" N –99° 52' 40" W, 1054 (RWA 6389); 22° 28' 30" N-99° 46' 35" W, 1035 (RWA 5759); 22° 48' 55" N-100° 28' 15" W, 1420 (RWA 5851); 22° 52' N-100° 09' 20" W, 1205 (RWA 6286); 23° 25' 15" N-100° 37' 40" W, 1600

(RWA 5723); 23° 49' N-100° 33' W, 1829 (RWA 5123-27). **Tamaulipas** 22° 50' 20" N-99° 52' W, 1120 (RWA 5850). **Zacatecas** 4.2 rd km NW La Pendencia (UTEP 9416); 4.3 km NE Pozo de San Juan, 2164 (RWA 1794); 10 km SE San Juan de los Charcos (UTEP 4558); 24° 29' 58" N-101° 17' 25" W, 1829 (RWA 6542); 24° 30' 15" N-101° 18' W, 1853 (RWA 5706); 24° 39' N-101° 19' 10"

W, 1720 (RWA 5686); 24° 55' 30" N-102° 07' 58" W, 1676 (RWA 5943).

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